Timing, Magnitude, Rates, and Putative Causes of Predator Movement Between Cotton and Grain Sorghum Fields

J. R. PRASIFKA, K. M. HEINZ, AND C. G. SANSONE³

Biological Control Laboratory, Department of Entomology, Texas A&M University, College Station, TX 77843-2475

Environ. Entomol. 33(2): 282-290 (2004)

ABSTRACT Previous studies suggest grain sorghum, Sorghum bicolor (L.) Moench, acts as an early-season predator source for nearby cotton, Gossypium hirsutum L., in areas where their growing seasons overlap. However, few data exist on predator movement in this system, and proposed causes of movement have not been tested. Field studies in 2001 and 2002 addressed both issues. Predator marking with rubidium was employed to measure predator movement between equal-sized areas of cotton and grain sorghum at three stages of grain sorghum phenology. Concurrent manipulative experiments in field cages tested for effects of phenology and aphid levels on movement by Hippodamia convergens Guérin-Méneville, a common predator in this system. Results from 2001 showed cotton gained 2.7 predators for every one lost to adjacent grain sorghum but that the collective movement of predators was similar among the three periods examined. The coccinellids H. convergens and Scymnus loweii Mulsant moved preferentially into cotton and seemed responsible for the overall pattern of predator movement between crops. For predators moving from grain sorghum into cotton, estimated rates of dispersal (15.8-19.9 m/d) were found to be similar among all taxa studied. Cage experiments suggested both crop phenology and abundance of aphid prey in cotton and grain sorghum cause predator movement, but only the effect of phenology was consistent between years. These results support the idea that grain sorghum is a source of predators during cotton's early growth stages and suggest that grain sorghum may continue to contribute to natural enemy populations during later stages of cotton growth.

KEY WORDS conservation, Hippodamia convergens, Scymnus loewii, biological control

SURROUNDING VEGETATION DIRECTLY influences the abundance of generalist predators in agricultural fields (Altieri and Letourneau 1982). This connection to neighboring habitats is particularly important for annual crops, where standing vegetation is routinely destroyed and renewed according to a yearly cycle. Predators moving from these habitats act as the initial colonists to recently planted agricultural crops (Wissinger 1997), but surrounding areas may also be sources of recolonization when predator populations are decimated by the use of pesticides (Wratten and Thomas 1990). Although attention has generally been focused on the benefits of uncultivated habitats as sources of predatory arthropods (Thomas et al. 1991, Landis et al. 2000), predators may also move from one crop to another, particularly when the phenologies of the crops are not synchronized (Wratten and Thomas 1990, Bommarco and Fagan 2002).

One reported example of such predator movement between crops involves contiguously grown cotton, Gossypium hirsutum L., and grain sorghum, Sorghum bicolor (L.) Moench. Both crops are common across broad geographic ranges of the United States, with cotton grown across the southern states, whereas grain sorghum spans the central region from South Dakota to Mexico. This results in overlapping production ranges in several states, but most extensively in Texas, which typically ranks first and second in the production of cotton and grain sorghum, respectively (Texas Agricultural Statistics Service 1998, 2000, 2002). Several factors noted by Fye (1971, 1972) suggest that, in areas where both crops are produced, grain sorghum could serve as a source of predators to cotton. First, cotton and grain sorghum support similar groups of predator taxa, the adults of which are generally very mobile. Second, grain sorghum is not usually treated with pesticides, in part because it is a relatively pest tolerant crop. Last, grain sorghum reaches maturity early relative to nearby cotton fields. Fye (1972) hypothesized that this would result in large predator populations produced in grain sorghum that move into cotton during the late stages of grain sorghum phenology. The corollary noted by subsequent research-

¹ Current address: USDA-ARS Corn Insects and Crop Genetics Research Unit, Genetics Laboratory c/o Insectary, Iowa State University, Ames, IA 50011.

² E-mail: kmheinz@neo.tamu.edu.

³ Texas Cooperative Extension, Texas A&M University, 7887 U.S. Highway 87 North, San Angelo, TX 76901–9782.

ers (Robinson et al. 1972, Lopez and Teetes 1976, Prasifka et al. 1999) is that such predator movement would improve biological control in cotton.

Several studies have explored the issue of predator movement from grain sorghum to cotton using different methods. Studies have examined predator densities in cotton at increasing distances from adjacent strips of grain sorghum (Burleigh et al. 1973, Massey and Young 1975), compared predator densities over time in both cotton and sorghum (Fye 1971, Fye and Carranza 1972), or compared isolated cotton plots to those planted near grain sorghum (Robinson et al. 1972, Parajulee et al. 1997). Lopez and Teetes (1976) used fluorescent dust marking to examine predator movement into cotton, and Prasifka et al. (1999) also used dusts to mark predators in both crops, attempting to assess predator movement into and out of cotton.

Although most of these studies support the premise that grain sorghum acts as a source of predators to colonize nearby cotton, a basic understanding of predator movement in this system has not been achieved. For example, direct measurement of predator movement using mark-recapture methods had only been attempted twice. In both cases, inadequate numbers of predators were recovered to support generalizations about the timing, magnitude, or rates of predator movement between cotton and sorghum. Furthermore, whereas Fye (1971, 1972) asserted that plant maturity was the cause of movement, only one study (Prasifka et al. 1999) has examined the possibility that other factors may motivate predator movement. Results indicated that predator movement was correlated with high temperatures and low levels of aphid prey. However, because this study relied on correlations and not experimental manipulation, causality cannot be inferred directly.

To correct these shortcomings, modifications to previous research were necessary. First, protocols for the use of a trace element marker, rubidium, were developed for use in cotton and sorghum (Prasifka et al. 2001). This allowed relatively easy predator marking and assured an increase in the number of marked predators recovered. Second, experimental manipulations of the putative causes of predator movement were made under field conditions. With these changes in methodology, the following objectives were pursued: (1) to measure the timing, magnitude, and rates of predator movement between cotton and grain sorghum; and (2) to test possible causes of movement for a common predator in both crops.

Materials and Methods

Complementary field studies were conducted in the Southern Rolling Plains of Texas (study area $\cong 31.3–32.1^{\circ}\,N, 99.6–100.6^{\circ}\,W)$ during 2001 and 2002. The first study was designed to measure directly the movement of predatory arthropods between adjacent fields of cotton and grain sorghum. A second study was conducted to test putative causes of predator movement between cotton and grain sorghum. In both cases, three study periods per season were timed to the

soft-dough, hard-dough, and physiological maturity stages of grain sorghum phenology (Vanderlip 1993). At these stages, cotton development had reached roughly five to six true leaf, first one-thirds grown square, and first bloom stages, respectively. The sorghum stages selected span the processes of grain maturation and leaf senescence hypothesized to cause predator dispersal (Fye 1972).

Measuring Predator Movement. Each year, six sites were selected in Runnels County, TX. A site consisted of one cotton field and one grain sorghum field oriented with their rows parallel. Within each field, a plot 100 m long by 40 m wide (0.4 ha) was flagged. Plots began 10 m from the crop interface of cotton and grain sorghum and were inset at least 100 m from the adjacent field edge. At each site, one plot was further divided into three subplots 10, 20, and 50 m from the interface of the cotton and grain sorghum fields (Fig. 1). The study sites were organized spatially into three pairs, in which the distance between paired sites was less than that between unpaired sites. For example, in 2001, the distance between paired sites ranged from 3.7 to 5.2 km and 16.8–32.5 km for unpaired sites. Weather conditions (temperature, relative humidity, precipitation, wind speed, wind direction, and barometric pressure) were monitored at one site within each site-pair with a PortLog weather station (Rain-Wise, Bar Harbor, ME), recording at 1-h intervals.

At the onset of the three grain sorghum phenological stages noted above, foliar sprays of rubidium chloride (RbCl) were applied to mark predators. Rubidium is a ubiquitous element chemically similar to potassium but usually found at very low concentrations. This similarity allows rubidium to be incorporated into biological systems at moderate levels without harmful effects (Stimmann 1974, Knight et al. 1989, Johnson and Reeves 1995) and results in its vertical transmission between trophic levels (Graham et al. 1978, Johnson and Reeves 1995, Corbett et al. 1996). These properties permit augmentation of background rubidium levels to internally mark plants, herbivores, and natural enemies. Because rubidium is replaced by potassium in the diet, the mark is temporary for actively feeding insects (Shepard and Waddill 1976, Graham et al. 1978, Fleischer et al. 1986) and may allow multiple mark-recapture experiments to be conducted at a location in one season. To measure movement both into and out of cotton, three cotton fields (one site within each pair) and three grain sorghum fields were selected to receive a RbCl spray. In the selected fields, RbCl sprays were made with equipment as described in Prasifka et al. (2001) and applied as 200 g RbCl dissolved in 68 liters of water per 0.4-ha plot.

Predator sampling to recover rubidium-marked predators was conducted in the unsprayed plots 2, 3, and 4 d after the RbCl sprays in the adjacent plot. Each subplot (1 row by 100 m) was sampled for 40 personminutes per day using visual searches of plants. Only adults of insect predators were collected, but both immature and adult spiders were sampled. Predators were collected with double-chambered inhalation-type aspirators, and aspirator inner chambers (2-dram

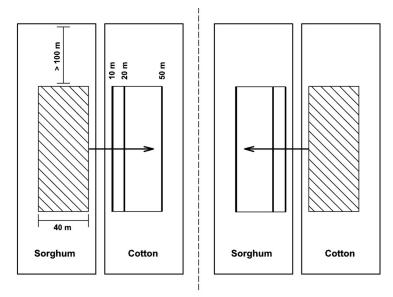


Fig. 1. Field plot arrangements for predator movement studies, 2001–2002. Dashed line separates sites where rubidium was applied to sorghum or cotton. Rubidium-treated plots are indicated by shading. Arrows indicate the predator movement measured. Numbers above unsprayed plots indicate the distance of sampling areas from the interface of fields. Diagram is not to scale.

screw cap vials) were capped and separated after completion of each subplot. Vials were then preserved in dry ice until they could be transported to the Biological Control Facility in College Station, TX, and placed in freezers before analysis.

In the laboratory, predators were sorted taxonomically into nine groups. Species (Hippodamia convergens Guérin-Méneville, Scymnus loewii Mulsant), genus (Orius spp., Notoxus spp., Collops spp., Geocoris spp., Nabis spp.), family (Chrysopidae), and order (Araneae) level groupings were used as needed, and all predators were separated as individual samples. Predators were then digested and analyzed for total rubidium content via atomic absorption spectrometry (AAS) as described in Prasifka et al. (2001), with two exceptions as noted below. The AAS technique measures the amount of light absorbed (at element-specific wavelengths) when a sample is heated to a temperature sufficient to generate free atoms of the element of interest. As made customary by Stimmann (1974), a predator was considered marked if its rubidium content in parts per million (PPM = μ g Rb/g predator dry mass) was at least 3 SDs above a control mean. Samples previously collected from the study area (Prasifka et al. 2001) were used as controls.

Changes made to the rubidium analysis were intended to improve accuracy and simplify methods. First, to minimize error, all samples were massed to microgram accuracy instead of using an average mass value for predators of the same group. Establishing precise mass values for each sample allowed an additional change in the methods used to test the rubidium mark status of spiders. Prasifka et al. (2001) used a size index to estimate mass values for noncontrol samples of spiders and regressed the rubidium content of con-

trols onto estimated mass values to construct an adjustable rubidium-mark threshold for spiders of various sizes. However, because the rubidium content per gram of spider mass (regardless of overall size) appeared constant, a single threshold was established using mass values and rubidium content of control samples from Prasifka et al. (2001). Consequently, spiders collected in 2001 and 2002 were evaluated using the same type of threshold (mean background + 3 SDs) as other predator groups. The interpretation of individual marked samples from spiders and the insect predators was straightforward; because predators were collected only from areas not treated with rubidium chloride sprays, all marked individuals were assumed to have recently moved from the adjacent field.

Statistical analyses were made using SAS software (SAS Institute 1999) with specific procedures as indicated. A two-factor analysis of variance (ANOVA; PROC ANOVA, including the two-way interaction) was conducted to assess if the magnitude of predator movement (sum of marked predators across all taxonomic groups) was explained by the time (phenology) and location (crop) of the collection. If main effects were found, additional analyses were used to determine which predator groups contributed to the main effects indicated by the ANOVA. Data from individual predator groups could not be transformed to meet normality or variance expectations of parametric statistics, so an $r \times c$ contingency table was used. This test was conducted once for each predator group (PROC FREQ, CHISQ option) and was based on both the number of marked individuals and the total number collected. For predator groups that moved into cotton in sufficient numbers $(n \ge 20)$, mean dispersal rates

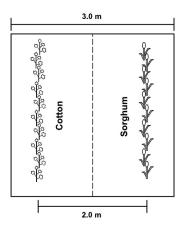


Fig. 2. Representation of cages and crops for assessing causes of movement, 2001–2002. Dashed line indicates the center of field cages. Dimensions indicated are to scale.

(m/d) were compared using a one-way ANOVA (PROC GLM). For these estimates, predators were assumed to have originated in the center of rubidiumtreated plots and were collected from a known location in the untreated plots. Accordingly, the distance between the middle row of the nearby rubidiumtreated plot and the row in which a predator collected was divided by the number of days since the rubidium spray to obtain an estimated dispersal rate.

Testing Causes of Movement. One site in Runnels County, TX, was selected each year to test putative causes of predator movement between crops. Fye (1971, 1972) and Prasifka et al. (1999) identified plant phenology, ambient temperature, and aphid density as putative causes of predator movement. Because manipulation of these variables could not be produced and replicated at a full scale, inclusion cages were used to simulate field conditions. These cages were used to test for effects of phenology and prey density on predator movement while temperature was monitored as an uncontrolled variable.

Alternating four-row strips of cotton and grain sorghum were planted (1-m row spacing), with cotton planted 40-45 d after grain sorghum. Shortly after cotton emergence, field cages measuring 3.0 by 3.0 by 2.0 m (length by width by height) were placed over the crops. The cages were covered with a Lumite mesh (20 by 20 holes/cm²; Synthetic Industries, Gainesville, GA) tight enough to prohibit the ingress or egress of the herbivores and natural enemies studied. Six cages placed only over cotton or sorghum were used for rearing of cotton aphid, Aphis gossypii Glover, or greenbug, Schizaphis graminum (Rondani), respectively. Another 24 cages were placed over three planted rows (two cotton, one sorghum). The middle row was removed, and the remaining plants were thinned to 10 of each crop at opposite sides of the cage (Fig. 2). To examine if climate differences caused by the cages might influence the behavior of predators released, during 2002, ambient temperature and relative humidity were measured both inside and outside

the cages by two HOBO H8 Pro Series data loggers (Onset Computer Corp., Bourne, MA) set to record at 1-h intervals.

An experimental protocol for the field cages was repeated at three different periods corresponding to the soft-dough, hard-dough, and physiological maturity stages of grain sorghum phenology. Before the start of each stage, cages were treated with chlorpyrifos (Lorsban-4E; Dow AgroSciences, Indianapolis, IN) at $1{,}100 \text{ g}$ (AI)/ha to eliminate existing pest and predator populations in the experimental cages. Seven days later, each experimental cage received one of four randomly assigned aphid treatments: aphids (S. graminum) on sorghum only, aphids (A. gossypii) on cotton only, aphids on both crops, or aphids on neither crop. On plants selected to receive aphids, a cut section of leaf with 15 of the appropriate aphid species (obtained from the aphid rearing cages) was pinned to one of the upper leaves with the aphids facing upward. This number of aphids was selected as representing a nonoutbreak aphid infestation level from field data collected during 1998 (J.R.P. and K.M.H., unpublished data). Within the next 24 h, both aphid species moved off the cut leaf sections and onto their intended host plants.

One day later, insectary-bought predators (Rincon-Vitova, Ventura, CA) of unknown age were released into the cages. Predators were shipped with coldpacks but without food or water. Before release, all predators were held under refrigeration without food for a maximum of 5 d and provided with moisture using a small piece of dental wick saturated with reverse osmosis-treated water. In 2001, 30 H. convergens and 40 O. insidiosus (Say) adults were released into each cage. No effort was made to measure or control sex ratio of the predators released. High mortality and small size contributed to inadequate recovery of O. insidiosus in 2001, so only H. convergens was used in 2002. Predator releases were made onto the upper leaves of plants, either cotton or grain sorghum, within each cage. Assignment of release location was made randomly within an aphid treatment so that three replicates of each of the eight aphid treatment X predator release combinations were created. Sampling of predators started 1 d after predator release. Predators collected from visual searches on cotton or grain sorghum plants were aspirated into separate vials. To detect excessive mortality or escapes, live predators found on the ground or other locations of the cage were aspirated into a third vial. Vials from each cage were placed in dry ice until transport to College Station, TX, where the number of recovered predators in each vial was counted.

As with the previous experiment, analyses of data from this experiment were made using SAS software (SAS Institute 1999). For data from each year, a three-way ANOVA (PROC GLM, including all two-way interactions) was used to test for the effects of crop phenology, aphid treatment, and predator release location on the recovery of *H. convergens* from caged cotton plants. To homogenize variance across treatments, recovery of *H. convergens* was assessed as the

Table 1. Predators collected and marked in cotton and grain sorghum, 2001

	Cotton		Sorghum		
Predators	Collected $(n = 2,331)$			Marked $(n = 166)$	
Hippodamia convergens	1,040	195	430	15	
Araneae	498	52	363	38	
Scymnus	357	98	139	11	
loewii					
Orius spp.	88	24	344	91	
Notoxus spp.	114	10	25	0	
Chrysopidae	108	35	11	1	
Collops spp.	78	25	30	8	
Geocoris spp.	36	1	24	0	
Nabidae	12	3	18	2	

proportion of lady beetles collected on cotton (relative to the total number of beetles recovered) in each cage, and this independent variable was arcsine square root transformed to meet assumptions of normality. When ANOVA results indicated an effect of phenology or treatment, Fisher least significant difference (LSD) procedure was conducted to separate means. To determine if weather conditions inside the cages were similar to those outside, mean temperature and humidity values (n = 30 d) were compared at six evenly spaced times during the day using a paired t-test.

Results

Measuring Predator Movement. The new rubidium mark threshold for spiders (based on 185 control samples) was 9.25 PPM. This value is intermediate to the thresholds established by Prasifka et al. (2001) that were used for other predator taxa in this study (range, 2.15–12.60 PPM). Overall, predator collections during 2001 yielded a total of 3,715 predators. Of these, 609 predators were marked with rubidium, indicating recent movement from an adjacent rubidium-treated plot. Cotton gained far more predators (443) than it lost (166) through an association with grain sorghum. The total numbers of predators collected and marked recoveries in each crop are shown sorted by taxonomic group in Table 1.

A two-way ANOVA indicated that the stage of phenology and crop in which collections were made did not adequately explain the variability in the number of marked predators recovered (F = 1.11; df = 5,12; P =0.407), but the F-test for the crop component only (F = 4.88; df = 1,12; P = 0.047) was significant (Fig. 3). Analysis of separate predator groups indicated that two groups moved preferentially into cotton, H. convergens ($\chi^2 = 57.87$, df = 1, P < 0.001) and S. loewii (χ^2 = 22.27, df = 1, P < 0.001). For all other groups, the hypothesis that the proportion of predators entering cotton was equal to the proportion leaving for adjacent plots of grain sorghum could not be rejected. Estimated dispersal rates of predators entering cotton fields ranged from 15.8 to 19.9 m/d (Table 2), but did not vary among taxa according to a one-way ANOVA (F = 1.17; df = 5, 423; P = 0.324).

Predator collections from 2002 produced 580 total predators, of which 34 were found to be rubidium marked. Rainfall collected by our weather stations ranged from 5.62 to 17.95 cm during the sampling dates at sorghum's soft dough stage. This caused extensive

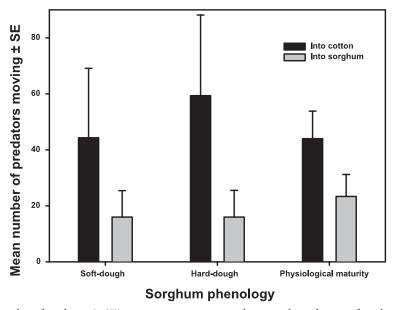


Fig. 3. Mean number of predators (\pm SE) moving into cotton or sorghum at indicated stages of sorghum phenology, 2001. A two-way ANOVA found differences (P < 0.05) between the number entering cotton and sorghum but not between stages of phenology.

Table 2. Estimated mean dispersal rates for predators immigrating into cotton, 2001

Taxon	Mean dispersal rate $(m/d) \pm SD^a$	Sample size (n)	
Hippodamia convergens	18.3 ± 7.9	195	
Scymnus loweii	17.3 ± 7.2	98	
Araneae	17.7 ± 5.2	52	
Chrysopidae	19.9 ± 8.3	35	
Collops spp.	19.0 ± 7.9	25	
Orius spp.	15.8 ± 7.8	24	

^a Estimates assume direct linear movement from centerline of rubidium-treated plots to collection point.

flooding in the region and prohibited any field collections of predators. When sorghum had reached maturity, additional rains of 1.58–3.68 cm created conditions unsuitable for rubidium spraying in three of the six locations. Compared with typical rainfall (mean \pm SE) for July in the Ballinger area over the previous 10 yr (2.59 \pm 0.66 cm; Office of the State Climatologist, Texas A&M University), these periods represented unusually high levels of precipitation. The resulting low sample sizes and unbalanced design prohibited statistical analysis of 2002 movement data.

Testing Causes of Movement. The temperature (t = 1.31, df = 5, P = 0.25) and relative humidity (t = -0.12, df = 5, P = 0.91) profiles inside and outside the field cages were similar during the duration of the study (Fig. 4). ANOVA results from 2001 indicated that phenology affected the recapture of H. convergens on cotton (F = 13.96; df = 2,54; P < 0.001). Means separation using Fisher LSD showed that a greater proportion of H. convergens was recovered from cotton

Table 3. ANOVA results for putative causes of predator movement, 2001-2002

Year	Factor	df	F	P
2001	Model (overall F-test)	17	2.65	0.003
	Phenology	2	13.96	< 0.001
	Aphid treatment	3	1.03	0.387
	Release location	1	1.60	0.212
	Phenology × aphid treatment	6	0.95	0.467
	Phenology × release location	2	1.17	0.318
	Aphid treatment \times release location	3	1.44	0.241
2002	Model (overall F-test)	17	7.04	< 0.001
	Phenology	2	36.01	< 0.001
	Aphid treatment	3	2.89	0.044
	Release location	1	25.01	< 0.001
	Phenology × aphid treatment	6	1.08	0.388
	Phenology × release location	2	1.71	0.190
	Aphid treatment \times release location	3	1.35	0.267

during the hard-dough and maturity stages of grain sorghum than at the soft-dough stage. No other factors or interactions were significant during 2001 (Table 3).

Phenology was also significant during 2002 (F = 36.01; df = 2,54; P < 0.001), again with a greater proportion of H. convergens collected on cotton during sorghum's hard-dough and maturity stages. The presence of a release location effect (F = 25.01; df = 1,54; P < 0.001) indicated that more beetles were recovered from cotton when they were initially released onto cotton. Finally, the effect of aphid density manipulations to cotton and sorghum plants was suggested by

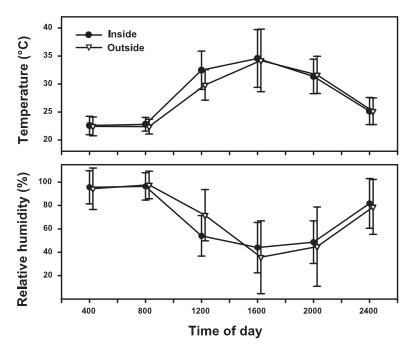


Fig. 4. Daily temperature (°C) and relative humidity (%) profiles inside and outside field cages during 2002. Values are presented as means (\pm SD) at 4-h intervals over the duration of the experiment (n = 30 d).

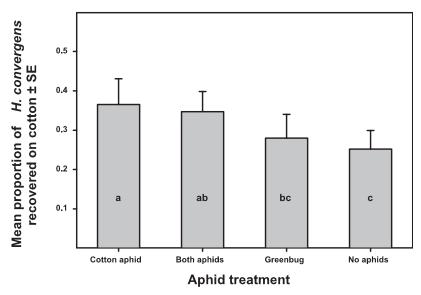


Fig. 5. Mean proportion of *H. convergens* collected on caged cotton plants, 2002. Aphid treatments containing the same letter do not differ. Data are presented as back-transformed means for ease of interpretation.

the ANOVA (F = 36.01; df = 2,54; P < 0.001) and examined by post-ANOVA analysis of the aphid treatments. Results showed a greater proportion of H. convergens was found on cotton when cotton aphids were present (with or without greenbugs present) than when no aphids were present in the cages. Recovery of H. convergens was also greater with cotton aphids only than with no aphids or greenbugs only (Fig. 5). Again, none of the two-way interactions tested were shown to be significant model components (Table 3).

Discussion

Results from predator marking experiments in 2001 showed that a greater number of predators moved into cotton than into sorghum while suggesting that movement of predators between the crops was unaffected by changes in grain sorghum phenology. These results agree with previous studies that showed enhanced predator levels in cotton adjacent to or intercropped with grain sorghum (Fye and Carranza 1972, Robinson et al. 1972, Burleigh et al. 1973, Massey and Young 1975, Parajulee et al. 1997, Parajulee and Slosser 1999, Prasifka et al. 1999). Data revealed a gain of 2.7 predators immigrating into cotton for each predator leaving for adjacent grain sorghum. This is surprisingly close the estimate of Prasifka et al. (1999), which noted a predator gain-to-loss ratio in cotton of 2.0 with a sample size of marked predators roughly 1/20th of the current study. Subsequent analysis of smaller predator groups indicated that the coccinellids H. convergens and S. loewii moved disproportionately from grain sorghum into cotton. Because these two species represented 60% (1,397/2,331) of all predators collected in cotton and 66% (293/443) of all marked predators moving into cotton from adjacent grain sorghum fields, it seems likely that coccinellids were

responsible for the overall pattern of predator movement into cotton during 2001.

Although no differences in 2001 predator movement were found over the three stages of phenology, this may be attributable to experimental design; replicates were located at relatively distant sites with crop planting and management under the control of cooperating growers. This arrangement was chosen in an effort to have results best reflect the conditions of crop management in the region, but may have resulted in greater variance in predator movement data. Previous studies suggesting the role of sorghum phenology have had more standardized conditions, with experiments unreplicated or pseudoreplicated at a single location (Fye 1971, Fye and Carranza 1972).

Data on the rate at which predators move from cotton into grain sorghum indicated mean dispersal rates from 16 to 20 m/d for all predator groups, and no differences between taxa were found. The indicated dispersal rates are likely underestimated because of difficulties associated with sampling; the experimental design only detects movement in the dimension perpendicular to the interface between the two fields (as indicated by arrows in Fig. 1), but does not detect movement parallel to the interface. However, the mobility indicated by the estimated dispersal rates suggests that the use of grain sorghum as a source of predators for cotton need not be confined to the small alternating strips of cotton and sorghum previously proposed (Robinson et al. 1972, Burleigh et al. 1973, Parajulee et al. 1997, Parajulee and Slosser 1999).

The lower number of marked predators recaptured during 2002 is not completely explained by the number of total predators collected. The percentage of marked predators as a fraction of all predators collected was markedly lower in 2002 (5.9%) than in 2001 (16.4%). It seems possible that precipitation on the

day of the final rubidium sprays may have interfered with the efficacy of our predator-marking technique if rubidium chloride was washed off plants before absorption could occur. This hypothesis is supported by the experimental results showing that foliar-applied rubidium may require 8–12 h for maximal absorption into plant tissues (Reickenberg and Pritts 1996).

Cage studies designed to test the hypotheses that aphid levels and phenology may motivate movement of H. convergens between crops showed an effect of phenology during both 2001 and 2002. Overall, a greater proportion of beetles was collected on cotton during the hard dough and maturity stages of sorghum. Because both crops matured over the study period, it is not immediately clear whether the growth of cotton rendered it more desirable as a habitat or if the gradual senescence of sorghum repelled H. convergens. However, because this effect was consistent across years whether predators were released onto cotton or sorghum (with no interactions), both of the above statements are probably true. In 2002, the combinations of aphid treatments to sorghum and cotton also influenced the proportion of beetles collected on cotton. Treatments with aphids on cotton had more H. convergens collected on cotton compared with when no aphids were present on either crop.

Based on the results from both years, it seemed that aphid levels and crop phenology both cause *H. convergens* to move between cotton and sorghum. Several species of Coccinellidae are known to respond through aggregration to high levels of aphid prey (Kareiva 1982, Ives et al. 1993), and recent evidence suggests that *H. convergens* accomplishes this response to prey levels by using olfactory cues from the aphids (Hamilton et al. 1999, Acar et al. 2001). However, results here suggest that *H. convergens* responds to relatively low levels of aphids on cotton and grain sorghum.

Alhough previous studies have suggested that an association of cotton and grain sorghum may have potential for improving cotton pest management, currently no purposeful use of grain sorghum is made with regard to arthropod pest management. This study confirms and quantifies the relationship of sorghum to cotton as a source of colonizing predators and indicates that both phenology and prey densities may motivate predator colonization of cotton. Because predators of all classes are competent dispersers, the use of grain sorghum as a predator source is not limited to the small-scale strategy of strip-cropping cotton and grain sorghum. A mosaic of cotton and grain sorghum fields over an agricultural landscape should be useful to improve early-season populations of predators in cotton and may also produce benefits as a source of predator recolonization if early-season pesticide applications to cotton are necessary. Grain sorghum will probably remain part of many cotton production systems as a rotation crop because of its tolerance to insect pests and drought, but to realize the full potential of improved pest management that may be provided in this system, further research on the impacts of predator movement on pest levels and cotton yields is needed.

Acknowledgments

We appreciate field assistance by A. Fry, H. Englert, and H. Keyser. C. Vasicek assisted in sorting and preparing samples for rubidium analysis. R. Minzenmayer provided invaluable aid in procuring research plots and timely field help. The manuscript was improved by suggestions and technical support from P. L. Anderson, K. Winemiller, J. Woolley, B. Mallick, P. C. Krauter, and anonymous reviewers. Research was funded by grants from Texas State Support Committee of Cotton Incorporated awarded to C.G.S., the Texas Higher Education Coordinating Board to K.M.H., and the Perry L. Adkisson Assistantship in Integrated Pest Management awarded to J.R.P.

References Cited

- Acar, E. B., J. C. Medina, M. L. Lee, and G. M. Booth. 2001. Olfactory behavior of convergent lady beetles (Coleoptera: Coccinellidae) to alarm pheromone of green peach aphid (Hemiptera: Aphididae). Can. Entomol. 133: 389–397.
- Altieri, M. A., and D. K. Letourneau. 1982. Vegetation management and biological control in agroecosystems. Crop Prot. 1: 405–430.
- Bommarco, R., and W. Fagan. 2002. Influence of crop edges on movement of generalist predators: a diffusion approach. Agric. For. Entomol. 4: 21–30.
- Burleigh, J. G., J. H. Young, and R. D. Morrison. 1973. Stripcropping's effect on beneficial insects and spiders associated with cotton in Oklahoma. Environ. Entomol. 2: 281–285.
- Corbett, A., B. C. Murphy, J. A. Rosenheim, and P. Bruins. 1996. Labeling an egg parasitoid, *Anagrus epos* (Hymenoptera: Mymaridae), with rubidium within an overwintering refuge. Environ. Entomol. 25: 29–38.
- Fleischer, S. J., M. J. Gaylor, N. V. Hue, and L. C. Graham. 1986. Uptake and elimination of rubidium, a physiological marker, in adult *Lygus lineolaris* (Hemiptera: Miridae). Ann. Entomol. Soc. Am. 79: 19–25.
- Fye, R. E. 1971. Grain sorghum. a source of insect predators for insects on cotton. Progr. Agric. Ariz. 23: 12–13.
- Fye, R. E. 1972. The interchange of insect parasites and predators between crops. PANS. 18: 143–146.
- Fye, R. E., and R. L. Carranza. 1972. Movement of insect predators from grain sorghum to cotton. Environ. Entomol. 6: 790-791.
- Graham, H. M., D. A. Wolfenbarger, and J. B. Nosky. 1978. Labeling plants and their insect fauna with rubidium. Environ. Entomol. 7: 379–383.
- Hamilton, R. M., E. B. Dogan, G. B. Schaalje, and G. M. Booth. 1999. Olfactory response of the lady beetle *Hippodamia convergens* (Coleoptera: Coccinellidae) to prey related odors, including a scanning electron microscopy study of the antennal sensilla. Environ. Entomol. 28: 812–822.
- Ives, A. R., P. Kareiva, and R. Perry. 1993. Response of a predator to variation in prey density at three hierarchical scales—lady beetles feeding on aphids. Ecology. 74: 1929-1938.
- Johnson, P. C., and R. M. Reeves. 1995. Incorporation of the biological marker rubidium in gypsy moth (Lepidoptera: Lymantriidae) and its transfer to the predator *Carabus*

- nemoralis (Coleoptera: Carabidae). Environ. Entomol. 24: 46–51.
- Kareiva, P. 1982. Predator-prey dynamics in spatially structured populations: manipulating dispersal in a coccinelid-aphid interaction, pp. 368–389. In S. A. Levin and T. G. Hallam (eds.), Lecture notes in biomathematics, vol. 54, mathematical ecology. Springer, Berlin, Germany.
- Knight, A. L., L. A. Hull, E. G. Rajotte, and S. J. Fleischer. 1989. Labeling tufted apple bud moth (Lepidoptera: Tortricidae) with rubidium: effect on development, longevity, and fecundity. Ann. Entomol. Soc. Am. 82: 481–485.
- Landis, D. A., S. D. Wratten, and G. M. Gurr. 2000. Habitat management to conserve natural enemies of arthropod pests in agriculture. Annu. Rev. Entomol. 45: 175–201.
- Lopez, E. G., and G. L. Teetes. 1976. Selected predators of aphids in grain sorghum and their relation to cotton. J. Econ. Entomol. 69: 198–204.
- Massey, W. B., and J. H. Young. 1975. Linear and directional effects in predator populations, insect damage, and yield, associated with cotton interplanted with corn and sorghum. Environ. Entomol. 4: 637–641.
- Parajulee, M. N., and J. E. Slosser. 1999. Evaluation of potential relay strip crops for predator enhancement in Texas cotton. Int. J. Pest Manag. 45: 275–286.
- Parajulee, M. N., R. Montandon, and J. E. Slosser. 1997. Relay intercropping to enhance abundance of insect predators of cotton aphid (Aphis gossypii Glover) in Texas cotton. Int. J. Pest Manag. 43: 227–232.
- Prasifka, J. R., K. M. Heinz, and C. G. Sansone. 2001. Field testing rubidium marking for quantifying intercrop movement of predatory arthropods. Environ. Entomol. 30: 711– 719.
- Prasifka, J. R., P. C. Krauter, K. M. Heinz, C. G. Sansone, and R. R. Minzenmayer. 1999. Predator conservation in cotton: using grain sorghum as a source for insect predators. Biol. Control. 16: 223–229.
- Reickenberg, R. L., and M. P. Pritts. 1996. Dynamics of

- nutrient uptake from foliar fertilizers in red raspberry (*Rubles idaeus* L.). J. Am. Soc. Hortic. Sci. 121: 158–163.
- Robinson, R. R., J. H. Young, and R. D. Morrison. 1972. Strip-cropping effects on abundance of predatory and harmful cotton insects in Oklahoma. Environ. Entomol. 1: 145–149.
- SAS Institute. 1999. SAS/STAT user's guide, version 8. SAS Institute, Cary, NC.
- Shepard, M., and V. H. Waddill. 1976. Rubidium as a marker for Mexican bean beetles, *Epilachna varivestis* (Coleoptera: Coccinellidae). Can. Entomol. 108: 337–339.
- Stimmann, M. W. 1974. Marking insects with rubidium: imported cabbageworm marked in the field. Environ. Entomol. 3: 327–328.
- Texas Agricultural Statistics Service. 1998. Texas agricultural statistics (1997). Tex. Agric. Stat. Serv. Bull. 256.
- Texas Agricultural Statistics Service. 2000. Texas agricultural statistics (1999). Tex. Agric. Stat. Serv. Bull. 258.
- Texas Agricultural Statistics Service. 2002. Texas agricultural statistics (2001). Tex. Agric. Stat. Serv. Bull. 260.
- Thomas, M. B., S. D. Wratten, and N. W. Sotherton. 1991. Creation of island habitats in farmland to manipulate populations of beneficial arthropods—predator densities and emigration. J. Appl. Ecol. 28: 906–917.
- Vanderlip, R. L. 1993. How a sorghum plant develops. Kans. Agric. Exp. Stn. Contribution 1203.
- Wissinger, S. A. 1997. Cyclic colonization in predictably ephemeral habitats: a template for biological control in annual crop systems. Biol. Control. 10: 4–15.
- Wratten, S. D. and C.F.G. Thomas. 1990. Farm-scale spatial dynamics of predators and parasitoids in agricultural landscapes, pp. 219–237. *In* R.G.H. Bunce and D. C. Howard (eds.), Species dispersal in agricultural habitats. Belhaven Press, London, UK.

 $Received for publication~28\,March~2003; accepted~17~October~2003.$